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The relationship between the osmotic concentration of leaf sap and height of leaf insertion in trees

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(WITH FOUR DIAGRAMS)

I. INTRODUCTION

The ascent of sap in trees presents a problem of such complexity that no one kind of observation is sufficient for its solution. Final conclusions must be based upon the comparison and correlation of careful measurements of all possible variables.

The rôle to be attributed to the osmotic concentration of the fluids of the leaf cells, like other possible factors in the rise of the transpiration stream, is still subject to marked differences of opinion.

One of the simplest and most direct methods of approaching the problem of the relationship between the concentration of the leaf sap and the movement of the transpiration stream is to determine whether leaves originating at a greater distance from the source of water absorption exhibit a higher osmotic concentration than those inserted nearer the source of intake. The importance of such determinations has been recognized by Ewart, Dixon and Atkins, Hannig and others.

Ewart was one of the first, if not the first, to attempt the determination of the osmotic concentration of the leaf sap at different levels. In 1905 he* thought he had demonstrated by plasmolytic methods that the concentration of the leaf sap increases from

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* Ewart, A. J. The ascent of water in trees. Phil. Trans. Roy. Soc. Lond. B. **198**: 41–86. 1905.

lower to higher levels. Later* he returned to the same problem, only to conclude that the sources of error in the use of the plasmolytic method are so great that it was idle to go farther with the study on the basis of the technique then available. After mentioning certain of the difficulties he says:

> "It is more correct therefore to use the term 'plasmalyzing concentration' for results obtained in this manner, and a series of observations for leaf cells of species of *Acacia, Eucalyptus,* and *Orevillea* taken from 1–12 meters high show that the concentration may vary from 2–6 per cent. KNO_3 in one and the same plant, and that the variation between leaves at the same level is at first as great as between leaves at different levels, and that the size of the cell and the age of the leaf appear to influence the plasmolytic concentration more than any other factors apart from food storage and assimilation. Hence this promising line of investigation into the problem of the ascent of sap must be abandoned as inaccurate and misleading."

The only exact published data of which we are aware are those furnished by Dixon and Atkins.†

Dixon in his volume on the Ascent of Sap‡ republishes these data with the same interpretation. Working with untreated leaves§ of *Magnolia acuminata, Fraxinus excelsior* and *Vitis Veitchii* they secured seven pairs of determinations, from which they conclude:

> "It here appears that, on the whole, taking the experiments in pairs, the leaves at the lower level contained sap with a lower (sometimes considerably lower) osmotic pressure than that of higher leaves. But the experiments are far from satisfactorily bearing out this view; for it will be noted that the osmotic pressure of the sap from leaves at the same level, but at different times and under different conditions, by no means corresponds in each case, although it is often higher than that of leaves at a lower level. The reverse, however, is sometimes found, as in expt. 6 and 7 where the pressure in the lower is much greater than in the higher leaves."

Dixon and Atkins recognized the fact that a relationship between the concentration of the sap of leaves inserted at different distances from the root system might be due to an adjustment to resistance in the conducting system as well as to the hydrostatic head. They found a slightly greater depression of the freezing point for sap from the more distantly placed leaves. From determinations on *Ulmus campestris* they conclude, however, that the resistance of the water tracts is not the controlling factor but that variation in osmotic concentration is to be attributed principally to the fluctuations in the sugar content due to differences in illumination.

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* Ewart, A. J. The ascent of water in trees, II. Phil. Trans. Roy. Soc. Lond. B. **199**: 341–392. 1906.

† Dixon, H. H., & Atkins, W. R. G. On osmotic pressures in plants; and on a thermo-electric method of determining freezing points. Sci. Proc. Roy. Dublin Soc. N. S. **12**: 275–311. 1910. Also in Notes, Bot. Sch. Trin. Coll. Dublin **2**, 1910.

‡ Dixon, H. H. Transpiration and the ascent of sap in plants. London, 1914.

§ This work was carried out before the necessity for the preliminary freezing of tissues was discovered by Dixon and Atkins. Possibly some of the inconsistencies in their results are due to this fact.

As a final conclusion they state:

> "Variation in pressure is not defined by the height of the leaves above the ground, nor by the resistance of the conducting tracts supplying the leaves. In each case the osmotic pressure was much greater than the tension of the water-supply could have been."

Thus the studies of Ewart leave the fundamental question of the existence of a differentiation in osmotic concentration associated with height quite unanswered, and the careful measurements by Dixon and Atkins are not adequately numerous for a final answer.

Conclusions have been drawn quite contrary to those resulting from the masses of data to be presented below. Thus Hannig* in the introduction to his study of osmotic concentration in root and leaf concludes that the work of Ewart and of Dixon and Atkins shows that "die Differenzen in der osmotischen Werten der Blattzellen einer Baumes von der Höhe des Blattansatzes unabhängig sind."

A proposal to investigate the concentration of the sap of leaves inserted at different levels is frequently met by the objection that the leaves at various heights are really subject to distinct environmental conditions (insolation and air movements) and that these external factors will either obscure any relationship, or, on the other hand, if a relationship between height and concentration be actually found, serve to fully explain it.

To us it has seemed that the primary task, the execution of which should precede all others, is to determine whether as a matter of fact there is a relationship between the level of origin of leaves and the properties of their sap. If there is no such interdependence, it is idle to advance theories in explanation of it, as some botanists seem inclined to do. If, however, careful sets of determinations show that a consistent relationship between height at origin and the osmotic concentration of the leaf sap does obtain, then, and only then, will it be worth while to inquire whether this relationship is of the magnitude necessary to overcome the weight due to the hydrostatic head and the resistance due to the conducting tracts, to measure the various environmental factors with a view to correcting for their influence upon sap properties, and to consider what is the most suitable biological interpretation of the observed relationship.

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* Hannig, E. Untersuchungen über die Verteilung des osmotischen Drückes in der Pflanze in Hinsicht auf die Wasserleitung. Ber. Deutsch. Bot. Ges. **30**: 194–204. 1912.

II. MATERIALS AND METHODS

We took our samples* from trees growing both in the open and in the woods. In collecting the samples we tried to secure them from branches exposed, as nearly as possible, to comparable atmospheric conditions. Such trees are not easy to find, however, and until actual instrumentation for light intensity and for the evaporating power of the air is carried out we shall make no claims whatever for freedom from such influences. In a few cases, indeed, we included trees which for some reasons were desirable, but suffered from lack of uniformity of exposure to light and air. Thus the tree of *Quercus Prinus* was higher than the surrounding vegetation, and the lower branches were somewhat more shaded than the upper ones. The leaves of *Betula lutea* collected July 23 from branches 66 feet above the ground were certainly more intensely illuminated than those at 52, 39, 25 or 11 feet.

In collecting samples of leaves, branches were lopped off at the respective heights and samples of the leaves were picked off as quickly as possible and enclosed in large test tubes which were taken to the laboratory for preliminary freezing* in order to facilitate the extraction of samples of sap really representative of the whole mass of tissue, as demonstrated by Dixon and Atkins† and confirmed by experiments made subsequently by ourselves.‡ The freezing-point lowering of the expressed sap, cleared by centrifuging at high speed,§ was determined by the use of a mercury thermometer graduated in hundredths of degrees in divisions sufficiently large to permit of estimation to thousandths of degrees. The freezing of the sap sample was effected by bubbling a dried air current through carbon bisulphide or ether in a Dewar bulb.

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* In undertaking these studies, we were concerned primarily with securing samples of leaves originating at different levels above the ground. We neglected, therefore, any measurement of the length of branch through which the sap would have to pass after leaving the trunk of the tree. Thus it is not possible to discuss in any exact way the possible influence of the resistance of conducting tracts on the magnitude of the concentration of the sap. Any errors due to this source may probably be disregarded in a preliminary study like the present. In a few cases we secured determinations from leaves originating on horizontal branches at different distances from the main trunk, but almost without exception these materials are open to some objection, and we have excluded them.

The table of constants contains the depression of the freezing point in degrees centigrade, Δ, corrected for the influence of undercooling, and the corresponding values of the osmotic pressure, P, from a published table.||

Specific conductivity at 30° C., κ, was determined in a Freas conductivity cell by means of the ordinary Wheatstone bridge of the physiological laboratory. The cell was standardized with $N/10$ KCl, considered as having a specific conductivity of 0.01412 at 30°.

Freezing point lowering, Δ, and specific conductivity, κ, are the two directly determined constants. Osmotic concentration or osmotic pressure, P, has been determined from Δ, and included in the table, partly because it is easier for some botanists to think in terms of atmospheres than in those of freezing point lowering, and partly because this is necessary for the purpose of ascertaining whether the increase of osmotic concentration with increase of height of insertion is at the rate which would be expected if this

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* Gortner, R. A., & Harris, J. Arthur. Notes on the technique of the determination of the depression of the freezing point. Plant World **17**: 49–53. 1914.

† Dixon, H. H., & Atkins, W. R. G. Osmotic pressures in plants. I. Methods of extracting sap from plant organs. Sci. Proc. Roy. Dublin Soc. N. S. **13**: 422–433, 1913. Also in Notes, Bot. Sch. Trin. Coll. Dublin **2**: 154–163. 1913.

‡ Gortner, R. A., Lawrence, J. V., & Harris, J. Arthur. The extraction of sap from plant tissue by pressure. Biochem. Bull. **5**: 139–142. 1916.

§ Some of the saps cannot be perfectly cleared by centrifuging.

|| Harris, J. Arthur, & Gortner, R. A. Note on the calculation of the osmotic pressure of expressed vegetable saps from the depression of the freezing point, with a table for the values of P for $\Delta = 0.001° - 2.999°$. Amer. Jour. Bot. **1**: 75–78. 1914.

increase were an adjustment on the part of the cells to hydrostatic head and to increased resistance of conducting tracts.

Freezing point lowering furnishes a measure of the concentration in moles and ions of all the solutes, non-electrolytes and non-dissociated and dissociated electrolytes. Specific electrical conductivity furnishes a measure of the concentration of dissociated electrolytes only.

It would be highly important to differentiate the electrolytic and the non-electrolytic elements in the solutes to which the whole of the concentration in moles and ions is due. Such differentiation presents, however, in the case of a mixed solution of non-electrolytes and of electrolytes composed of inorganic salts and of weakly dissociable organic salts and acids, a problem of great difficulty. We have therefore contented ourselves with the calculation of the ratio κ/Δ, which is useful although obviously only a substitute for more refined analysis.

Before proceeding to the analysis of the results, a word should be said concerning the trustworthiness of the constants.

There are two sources of error: the probable errors of random sampling in the collection of the leaves and the technical errors in the extraction of sap and in the determination of the constants. The determination of the actual magnitude of these errors presents a problem of considerable difficulty, and we are not in a position to say exactly how large they may be. It is quite clear from the consistency of our results that they are not so great as to obscure the general law, the existence or the non-existence of which we have been seeking to demonstrate.

We do not, however, lay emphasis upon any single constant or difference, and we do not attempt to explain individual inconsistencies. In the rather onerous task of collecting material for and carrying out the determination of 72 freezing points and 66 conductivities, it is highly improbable that we should have been able to avoid entirely probable errors of random sampling in the collection of the tissues and errors of laboratory technique at least as great and sometimes greater than the actual differences of the kind which we have been seeking to demonstrate, if existent.

Thus, even if osmotic concentration increases with height of insertion, one should expect to find a negative relationship indicated by actual measurements occasionally, just as in other instances the increase indicated by the constants would be higher than the true value.*

III. PRESENTATION AND ANALYSIS OF DATA

Altogether 26 sets of determinations were made, covering 12 species of trees. All collections were made in the immediate neighborhood of the Station for Experimental Evolution. The results are given in the accompanying tabular statement.

Here are given the approximate actual heights above the ground of the samples of leaves taken, designated by letters A, B, C, $\cdots$ from the highest to the lowest, the depression of the freezing point, Δ, and the osmotic concentration or pressure in atmospheres, P, specific electrical conductivities, κ, multiplied by 10^5 and $\kappa/\Delta \times 10^5$ of the expressed leaf sap.

These results in terms of osmotic concentration, P, are represented in DIAGRAMS 1 and 2, which are self-explanatory.

A cursory examination of the protocol or a glance at the diagrams shows that almost without exception the osmotic concentration is higher in samples taken at the higher levels.

As a means of more exact comparison we have determined the difference in these values for every possible pair of levels, i. e., $1/2n(n - 1)$ sets of differences for each tree, where n is the number of levels from which samples were taken. These differences are taken (constant for higher level) less (constant for lower level).

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* A particular case in point is that of two determinations based on a tree of *Populus balsamifera*. A first pair of collections made on August 25, indicated that the leaves taken from the 6-foot level contained sap which froze at 0.042° lower than that of leaves from the 25-foot level. A repetition of the collections on August 28 indicated that the sap of the leaves from the 22-foot level froze 0.105° higher—i. e., had 1.26 atmospheres higher osmotic pressure—than those at the 6-foot level.

Note that if these two determinations be averaged, they indicate a higher osmotic concentration for the samples taken at the higher level. Since, however, the two are not consistent we have omitted both. Possibly this tree should not have been used at all since the collections from the lower branches were made from the ends of long branches at a considerable distance from the main trunk. Thus if the resistance of the conducting tracts be a factor of importance it would tend to minimize the difference between the two determinations.

† In two of the determinations based on *Juglans* and in two or more of those based on *Robinia*, collections were made from the same trees in 1914 and 1915. Otherwise all are based on different individuals.

Sample	Height	Δ	P	$\kappa \times 10^5$	$\kappa/\Delta \times 10^5$
Acer rubrum L. June 10, 1915					
A.........	47	1.385	16.66	863	623
B.........	27	1.359	16.35	911	671
C.........	12	1.334	16.05	938	703
Acer rubrum L. August 25, 1915					
A.........	50	1.210	14.56	896	741
B.........	38	1.131	13.61	938	830
C.........	10	1.084	13.04	834	770
Acer rubrum L. August 25, 1915					
A.........	43	1.046	12.59	852	815
B.........	13	.992	11.94	915	922
Betula lenta L. August 1, 1915					
A.........	29	1.518	18.25	1,056	696
B.........	12	1.411	16.97	1,160	822
Betula lenta L. August 23, 1915					
A.........	40	1.046	12.59	——	——
B.........	17	.933	11.23	——	——
Betula lenta L. August 23, 1915					
A.........	46	1.182	14.22	——	——
B.........	13	1.090	13.12	——	——
Betula lutea Michx. July 23, 1914					
A.........	66	1.293	15.55	1,160	897
B.........	52	1.331	16.01	1,027	772
C.........	39	1.257	15.12	1,110	883
D.........	25	1.173	14.11	1,083	923
E.........	11	1.050	12.63	990	942
Fagus grandifolia Ehrh. August 20, 1915					
A.........	64	1.824	21.92	——	——
B.........	19	1.441	17.33	——	——
Fagus grandifolia Ehrh. August 25, 1915					
A.........	43	1.493	17.95	1,278	856
B.........	15	1.402	16.86	1,252	893
Juglans cinerea L. June 18, 1914					
A.........	52	1.522	18.31	1,046	687
B.........	44	1.525	18.33	1,114	731
C.........	38	1.429	17.18	1,218	852
D.........	32	1.513	18.19	1,174	777
E.........	21	1.484	17.85	1,197	807
F.........	8	1.398	16.81	1,332	954

Sample	Height	Δ	P	$\kappa \times 10^5$	$\kappa/\Delta \times 10^5$
Juglans cinerea L. June 4, 1915					
A.........	41	1.209	14.54	1,208	999
B.........	30	1.137	13.68	1,232	1,084
C.........	17	1.131	13.61	1,213	1,072
Juglans cinerea L. June 8, 1915					
A.........	45	1.049	12.62	1,435	1,368
B.........	24	1.015	12.21	1,252	1,234
Gleditschia triacanthos L. August 25, 1915					
A.........	46	1.419	17.07	927	653
B.........	15	1.285	15.46	938	730
Platanus orientalis L. August 28, 1915					
A.........	66	1.353	16.27	1,458	1,078
B.........	45	1.267	15.24	1,627	1,284
C.........	21	1.127	13.56	1,588	1,409
Quercus coccinea Wang. June 30, 1914 *					
A.........	56	1.592	19.14	981	617
B.........	33	1.383	16.63	848	613
Quercus palustris L. June 16, 1914					
A.........	33	1.932	23.22	903	467
B.........	23	1.728	20.77	1,002	580
C.........	9	1.681	20.21	1,057	629
Quercus Prinus L. June 16, 1914					
A.........	47	1.683	20.23	1,123	667
B.........	36	1.670	20.08	1,283	768
C.........	30	1.640	19.72	1,314	801
D.........	19	1.628	19.57	1,288	791
Robinia Pseudacacia L. June 9, 1914					
A.........	45	1.050	12.63	1,536	1,463
B.........	12	.902	10.86	1,458	1,616
Robinia Pseudacacia L. June 9, 1914					
A.........	45	.969	11.66	1,232	1,272
B.........	36	.932	11.22	1,267	1,360
C.........	24	.915	11.01	1.362	1,488
Robinia Pseudacacia L. June 12, 1914					
A.........	51	1.034	12.44	1,277	1,236
B.........	39	.920	11.07	1,181	1,285
C.........	29	.903	10.87	1,217	1,348
D.........	9	.887	10.68	1,340	1,511

* In the cases of *Quercus coccinea* of June 30, samples taken at 61 and at 50 feet proved insufficient for a determination of freezing point lowering and have been combined to form a single sample arbitrarily placed at 56 feet.

Sample	Height	Δ	P	$\kappa \times 10^5$	$\kappa/\Delta \times 10^5$
Robinia Pseudacacia L. JUNE 18, 1914					
A	41	1.158	13.93	1,512	1,306
B	18	1.045	12.57	1,589	1,521
Robinia Pseudacacia L. JUNE 14, 1915					
A	40	1.189	14.30	1,379	1,159
B	28	1.126	13.55	1,407	1,249
C	14	1.017	12.24	1,213	1,193
Robinia Pseudacacia L. JUNE 8, 1915					
A	30	.876	10.54	1,061	1,212
B	13	.817	9.84	1,390	1,701
Robinia Pseudacacia L. JULY 30, 1915					
A	37	1.009	12.14	1,390	1,377
B	25	.960	11.55	1,424	1,483
C	8	.998	12.01	1,298	1,301
Salix sp. JUNE 8, 1915					
A	25	1.029	12.38	1,605	1,560
B	10	1.024	12.32	1,599	1,562
Salix sp. JUNE 8, 1915					
A	33	1.180	14.20	1,567	1,328
B	12	1.171	14.09	1,574	1,344

Thus the signs are positive when osmotic concentration increases with height of insertion.

For example, in the case of *Acer rubrum* of June 10 the differences are:

Heights	$L-L_0$	Δ	P	$\kappa \times 10^5$	$\kappa/\Delta \times 10^5$
$A-B$	20	0.026	0.31	-48	-48
$A-C$	35	0.051	0.61	-75	-80
$B-C$	15	0.025	0.30	-27	-32

It is quite unnecessary to burden these pages with the actual differences, which have been represented graphically in the diagrams. Summarizing the results we note first of all that in 73 of the 78 comparisons which may be made, the sample of tissue collected at the higher level shows a greater concentration than does the one taken at the lower level. More satisfactory evidence of an increase in the concentration of the leaf sap with increase in height of insertion could hardly be desired!

On the assumption of the adjustment of the leaf cells to an increased load—an assumption which we are not at this moment either urging or combating—the increase in osmotic concentration of the sap of the tissues collected at a higher level, L, over that of tissues collected at a lower level, L_0, should be proportional to the combined weight of two factors: (*a*) the hydrostatic head,

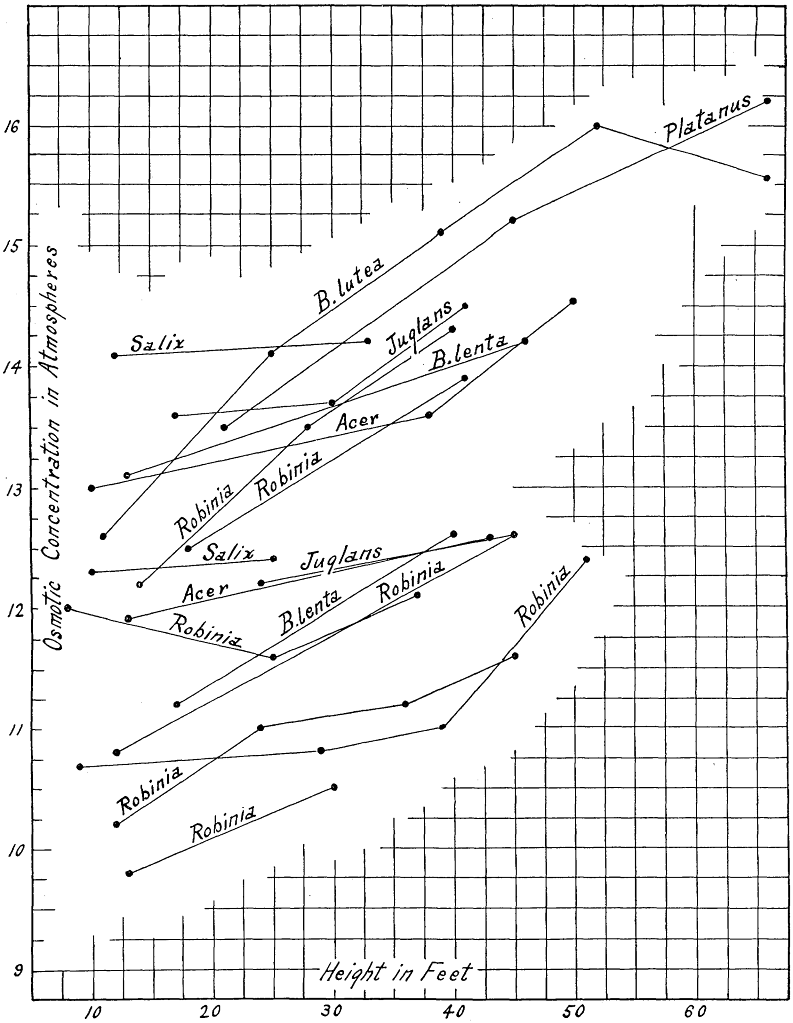

DIAGRAM I

and (*b*) the resistance due to the passage of the column of water of length $L - L_0$ through the conducting tracts.

Since $L - L_0$ is measured in feet, both of these values should be expressed in heights of water column in the same units. Thus the increase in atmospheres pressure due to hydrostatic head, H, should be given by

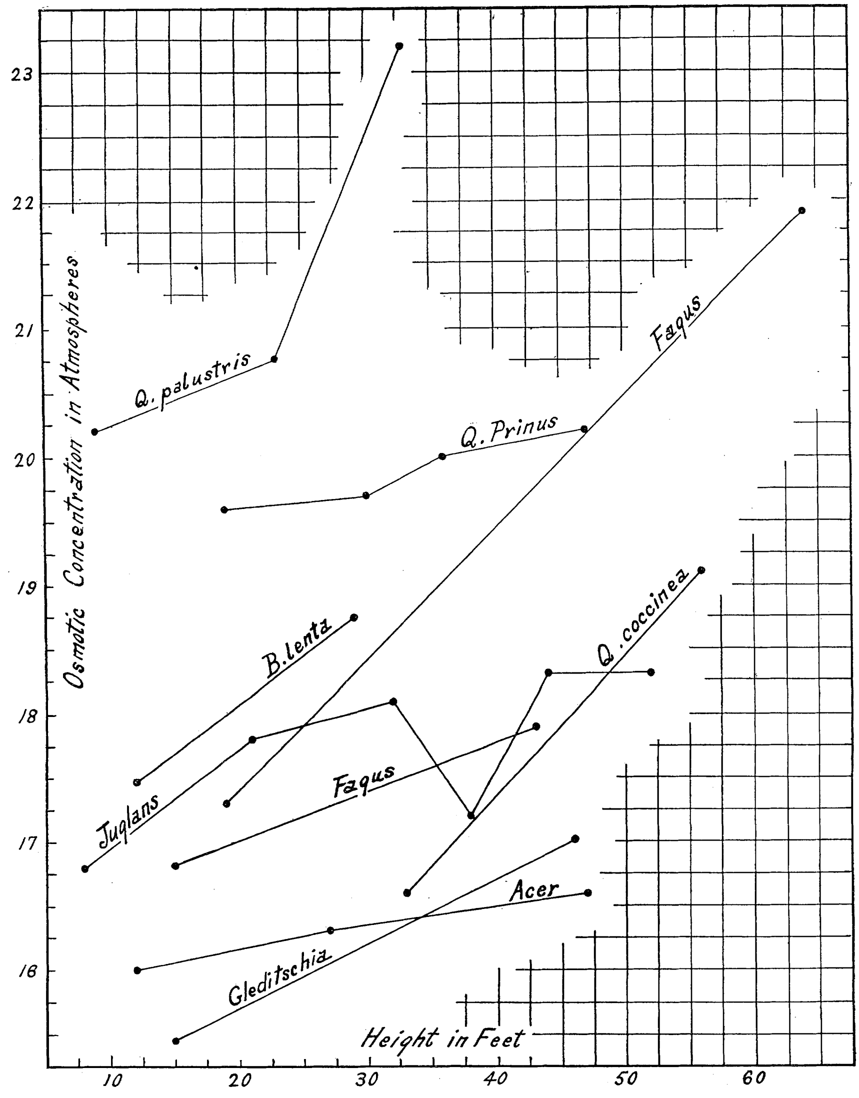

DIAGRAM 2

$$P - P_0 = H,$$

where

$$H = (L - L_0)/34,$$

where except for differences due to the elevation above sea level at which collections are made, H is invariable.

The resistance of the conducting tracts may be most conveniently expressed in terms of the ratio between (1) height of a column of water, R', which is required to force water through a horizontal stem of length $L - L_0$ at the rate of the transpiration stream, and (2) the height of a column of water which is the equivalent of one atmosphere pressure, i. e., $R = R'/34$.

Possibly R, the constant for the resistance of the conducting tracts, may differ from species to species. However this may be, workers who have attempted to determine the value of this constant have come to widely divergent conclusions.

Dixon devotes Chapter VI of his book on Transpiration and the Ascent of Sap to the criticism of the experimental data on the resistance offered by the wood to the movement of the transpiration stream. He concludes:

> "It appears that water may be moved through a stem in a horizontal position with the velocity of the transpiration current if urged by a head equal to the length of the stem. To raise water in a vertical stem at the same velocity, evidently twice the head will be required. Consequently when the force is applied as tension at the upper end, the greatest stress the water need be subjected to is double the height of the moving column."

Now while we may assume that

$$P - P_0 = H + R$$

represents approximately the two most important factors determining any adjustment (if such adjustment really exists) of the cells to increased load, it is quite clear that the equation may not be so simple. Other factors are probably also involved. For example capillarity may diminish the downward pull due to gravity. Possibly the power of imbibition of the leaf colloids may also play a rôle similar to that of the osmotic concentration of the solutes which contribute to the freezing-point lowering.

It is clear that the testing of the experimental results secured in our height studies against this formula is rendered highly questionable by reason of the fact that nothing is definitely known concerning the value of R in the species of trees with which we have worked.

The average ratio of the differences in height of all the possible pairs of samples from the same individual tree to the water-column equivalent of one atmosphere have been computed and found to be

$$\bar{H} = \overline{(L - L_0)/34} = 0.646.$$

Thus if differences in hydrostatic head stood in a causal relation to differences in the osmotic concentration of the leaf sap, and were the only factor of significance, one would expect an average difference of 0.646 atmospheres in the series of differences determined from our observations.

Naturally the resistance of the conducting tracts cannot be neglected. Dixon estimates that at most this is not greater than the hydrostatic head. If twice this value be taken for the sake of obtaining concrete figures the theoretical mean value of the difference in osmotic concentration at two levels would be 1.291.

The observed mean difference in osmotic concentration, P, is almost exactly midway between the two values 0.646 and 2×0.646, i. e., 0.978 as compared with the mid value 0.968.

The closeness of agreement to be expected between observation and theory must depend entirely upon the value assigned to R. Taking $R = H$ the agreement is not good, for the mean value of $P - P_0$ is about 1.00 as compared with the expected 1.30. The value of R which would harmonize hypothesis and observation would be .333 as compared with .646, or about half the hydrostatic head instead of the equivalent of the hydrostatic head considered the maximum value by Dixon. Since determinations of the resistance of the conducting tissues have for the most part been made on cut branches and with methods in which errors are unavoidable, it seems quite possible that half rather than the equivalent of the hydrostatic head may be the true value of the force required to overcome the resistance encountered by water in moving through the conducting tracts of these species at the rate of the transpiration stream.*

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* Capillary rise in the stem and imbibition pressure in the leaf cells would both tend to offset R. Neither of these forces would be included, at least in their entirety, in the direct measurements of R which have been made.

It is perhaps evident from the preceding paragraphs that the four lines of investigation now most needful for a more complete understanding of the relationship between osmotic concentration and level of leaf insertion are: (*a*) more extensive measurements of the resistance opposed to the transpiration stream by the conducting tracts; (*b*) detailed investigations of the properties of the fluids of the transpiration stream at different levels in the trunk throughout the year; (*c*) measurements of the two chief atmospheric environmental factors, evaporating power of air and insolation at different levels; and (*d*) determination of the extent of the rôle played by the imbibition pressure of leaf colloids.

The question of the resistance of the wood system has been touched on above. Further measurements for a great variety of species are needed. The importance for plant physiology in general of the investigation of the composition of the transpiration stream at different levels has been shown by Dixon and Atkins who have provided a method* and have published several series of measurements on trees examined during the winter and vernal season.† It seems rather improbable that such differences as they were able to demonstrate during the period of mobilization of reserve materials should be of great influence at the time at which our determinations were carried out. Nevertheless the subject deserves far more detailed study than Dixon and Atkins have been able to give it in their splendid pioneer work.‡

Differences in the evaporating power of the air and in insolation would (theoretically) influence osmotic pressure by increasing the concentration of solutes in the leaves by evaporation and through differences in the rate of photosynthesis in varying illumination.

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* Dixon, H. H., & Atkins, W. R. G. Osmotic pressures in plants. IV. On the constituents and the concentration of the sap in the conducting tracts, and on the circulation of carbohydrates in plants. Sci. Proc. Roy. Dublin Soc. N. S. **14**: 374–392. 1915. Also in Notes, Bot. Sch. Trin. Coll. Dublin **2**: 275–293. 1916.

† Dixon, H. H., & Atkins, W. R. G. Osmotic pressures in plants. VI. On the composition of the sap of the conducting tracts of trees at different levels and at different seasons of the year. Sci. Proc. Roy. Dublin Soc. N. S. **15**: 51–62. 1916. Also in Notes, Bot. Sch. Trin. Coll. Dublin **2**: 335–346. 1916.

‡ Note that Dixon and Atkins find that the concentration of carbohydrates increases from lower to higher levels of the trunk. Possibly this may have some relation to our own findings with regard to the increase of osmotic concentration but the decrease of conductivity, or at least of the ratio of conductivity to freezing point lowering, in leaves inserted at higher levels. See discussion below.

The question of differentiation in atmospheric conditions at various levels in the forest has long received the attention of ecologists. Thus as early as 1888 Schimper* called attention to differences in the epiphytic vegetation of the forest floor and canopy. Shreve in his studies on Jamaican Hymenophyllaceae† and on Jamaican montane rain forest epiphytes in general‡ has emphasized the same point, referring the observed differences to "vertical differences between the climate of the forest floor and its canopy."

Further light is thrown upon the subject by an examination of the specific electrical conductivity of the saps.

While the values of κ measuring the concentration of dissociated electrolytes do not show as great regularity as do those of Δ measuring the concentration of total solutes, the general trend of the relationship between this constant and height of insertion is clearly the reverse of that demonstrated by the freezing-point lowering. Thus in 46 cases the conductivity decreases§ from lower to higher levels as compared with 29 cases in which it increases.|| Thus apparently the saps from higher levels are actually less rich in electrolytes than those from the lower levels.

That samples from higher levels are relatively less rich in electrolytes is splendidly shown by a comparison of the ratios of electrical conductivity to freezing-point lowering, i. e., κ/Δ. These are represented in DIAGRAMS 3 and 4. In all but 13 of the 75 cases the ratio is lower in the saps from the higher levels. Further-

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* Schimper, A. F. W. Die epiphytische Vegetation Amerikas. Bot. Mitt. a. d. Tropen **1**, 1888.

† Shreve, F. Studies on Jamaican Hymenophyllaceae. Bot. Gaz. **51**: 184–209. 1911.

‡ Shreve, F. A Montane Rain-Forest. Pub. Carn. Inst. Wash. **199**: 38–41. 1914.

§ Botanists who are unaccustomed to thinking in physico-chemical terms need only remember that specific electrical conductivity is the reciprocal of the resistance which is inversely proportional to the concentration of ions of electrolytes. Thus a decrease in conductivity indicates a decrease in the concentration of dissociated electrolytes.

|| Confidence in the significance of these differences is increased by the fact that the mean value of the negative differences (i. e., those in which the conductivity at a lower level is greater than that at a higher level) is greater than that of the 29 positive differences.

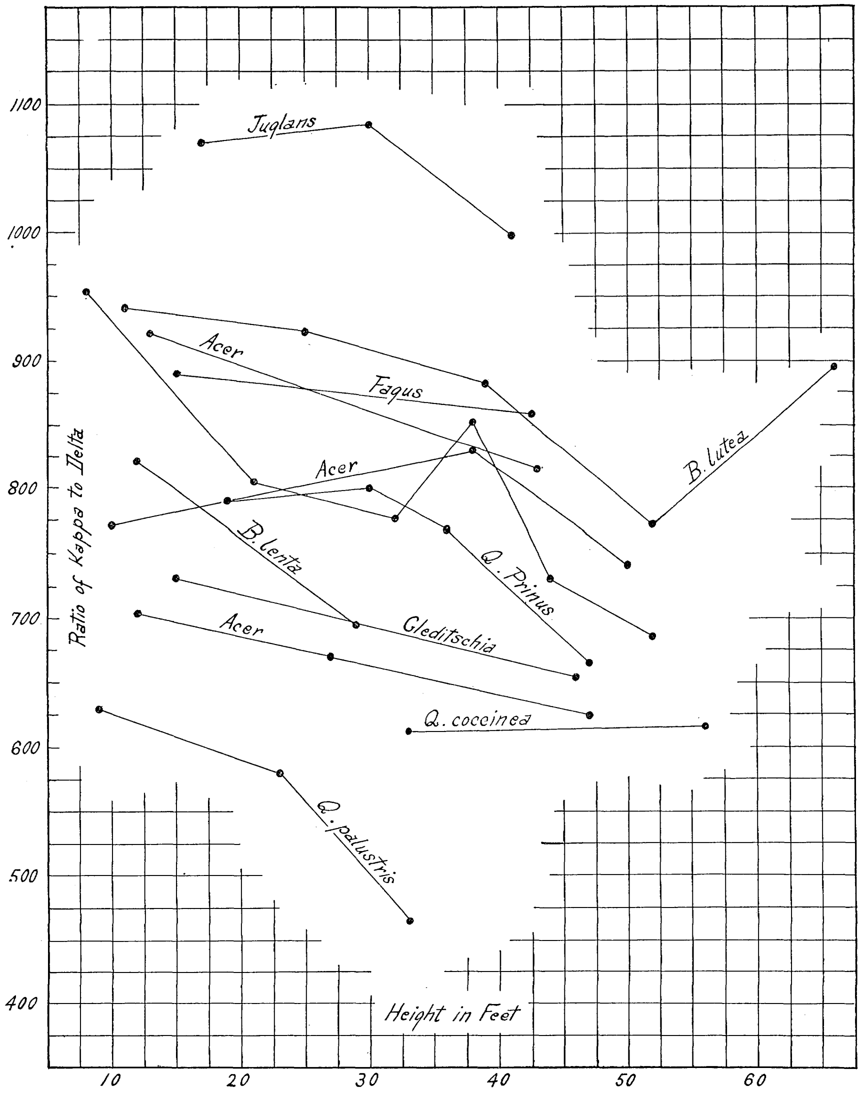

DIAGRAM 3

more, the averages of the negative differences is far higher than those indicating increase in κ/Δ with increase in height of insertion. Thus the mean of the positive differences between the values of $(\kappa/\Delta) \times 10^5$ for higher and lower levels is only 69.5 as compared

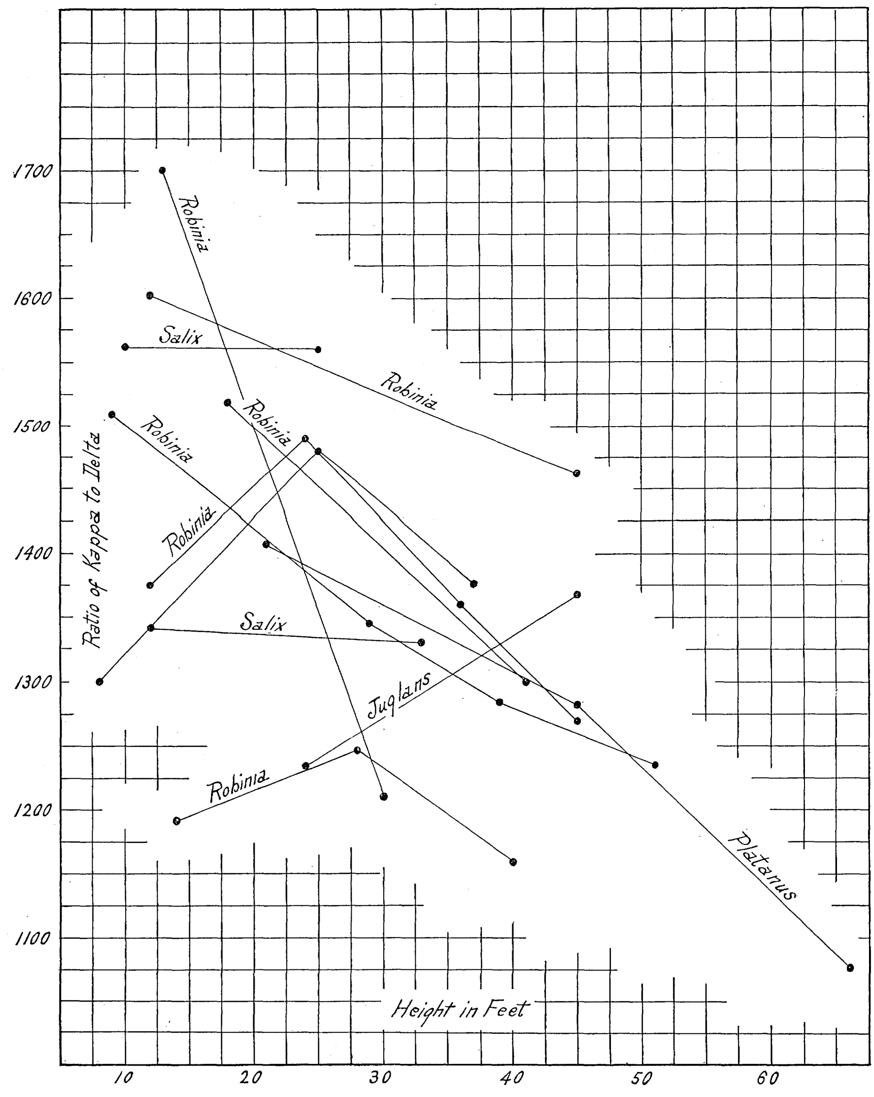

DIAGRAM 4

with a mean of – 112.3 for the negative differences. For all comparisons the mean differences in – 80.7.

Thus our findings apparently indicate that if environmental heterogeneity plays a rôle in the determination of the differences in the physico-chemical constants found, the increased photosynthesis at higher levels is the factor of the greatest importance.

Our own feeling in regard to the matter is that conclusions concerning this question should be deferred until actual measurements of the suggested environmental factors are available.

IV. RECAPITULATION

In the preceding pages we have considered the problem of the relationship between level of insertion and the physico-chemical properties of leaf sap in trees.

Measurements on 26 trees belonging to 12 species show that:

(*a*) The osmotic concentration of the leaf sap as determined by the freezing-point lowering method increases from lower to higher levels. This is true almost without exception.

(*b*) Specific electrical conductivity, κ, shows a tendency to decrease from lower to higher levels. The results are, however, by no means so regular as those for the depression of the freezing point, Δ.

(*c*) The ratio of specific electrical conductivity to freezing-point lowering, κ/Δ, decreases from lower to higher levels. This is true, almost without exception.

The relationship of physico-chemical properties to level of leaf insertion must be due to either internal or environmental factors.

The suggestion is made as a basis for further investigation that if the increase in osmotic concentration with increase in level of insertion be an adjustment on the part of the leaf cell to increased load, the increment in osmotic concentration should be approximately given by

$$P - P_0 = H + R,$$

where P is the osmotic concentration at a higher and P_0 that at a lower level, H is the weight in terms of atmospheres of a column of water $L - L_0$ in height, and R is the resistance, expressed in atmospheres, to the passage of water moving at the rate of the transpiration stream opposed by conducting tracts of the length $L - L_0$, where L and L_0 are the heights of the two levels of leaf insertion.

The ratio

$$\frac{P - P_0}{(L - L_0)/34},$$

which should equal unity within the limits of experimental error *if increase in osmotic concentration were an adjustment to hydrostatic head alone*, varies widely, with the average value of 1.508. This excess might be expected from the resistance due to the conducting tracts. The closeness of agreement of theory and observation must depend upon the value found for R, a value upon which experimenters are not at all in accord.

We must, however, point out that an agreement between the observed increments in osmotic concentration and the theoretical values calculated from the hydrostatic head and the resistance of the conducting elements cannot be taken as proof of an adjustment on the part of the cells to the back pull due to these factors. Such agreement might be purely accidental. Until the possible external factors to which increase in osmotic concentration at higher levels might be due are eliminated by experimental studies, any such agreement should be regarded as a coincidence. Measurements of the extent of differentiation in evaporating power of the air and in the intensity of illumination to which leaves growing at various heights are subjected are urgently needed.

In emphasizing the fact that the results of this study neither substantiate nor disprove the assumption that the back pull due to hydrostatic head and to the resistance of the tracts stand in a causal relation to the increase in osmotic concentration, we must point out that if osmotic concentration of the leaf sap be a factor of importance in the rise of the transpiration stream, the increase in the osmotic concentration with height of insertion may bear a very significant causal relation to the ascent of sap in trees.

The fact that the relative concentration of electrolytes decreases from lower to higher levels would indicate that the differences are due to increased photosynthesis in the upper regions of the tree rather than to the concentration of salts from the soil solution by increased transpiration.

In conclusion, it is perhaps hardly necessary to suggest the desirability of correlating differences already known to be associated with height in trees—for example, heavier fruiting or the development of the so-called shade leaves—with sap properties.

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